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The odyssey of new production

C.S. Yentsch[a], C.M. Yentsch[a,b,*], D.A. Phinney[a], B.E. Lapointe[c], S.F.W. Yentsch[a]

[a] *Bigelow Laboratory for Ocean Sciences, McKown Point Road, West Boothbay Harbor, ME 04575, USA*
[b] *Mel Fisher Maritime Museum, Key West, FL 33040, USA*
[c] *Harbor Branch Oceanographic Institution, Fort Pierce, FL 34936, USA*

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Abstract

In studies of primary production of the open ocean, the measurement of new production is often considered a measure of the degree of eutrophication. Because of new research this is questionable, which in our opinion, calls for a refinement to the original concept. We believe that the measure of variable fluorescence is pivotal to a new understanding. Our research enforces the growing conviction that the measurement of Fv/Fm can be interpreted as an analogue for nutrient stress. We measured variable fluorescence in axenic cultures at the CCMP at the Bigelow Laboratory. The Fv/Fm of cultures, upon transfer to new media reached a maximum followed by a decline after approximately 30 days. The rate of decline does not appear to be species specific. Most of the clones remained relatively high after 30 days. The high Fv/Fm values observed in nutrient-replete cultures are not characteristic of the oligotrophic surface waters off Florida and the Bahamas, but are approached in the eutrophic waters of the Gulf of Maine. In contrast, Fv/Fm measurements of attached macroalgae and coral zooxanthellae are characteristically much higher than microalgae of either oligotrophic or eutrophic regions. Accordingly, we advance the case for interpretation of Fv/Fm in terms of nutrient stress in ecological studies and advocate that the old concept of new production should be modified.

Keywords: Variable fluorescence; Fv/Fm; New production; Nutrient stress; Ecology; Microalgae; Macroalgae; Coral zooxanthellae; Natural populations; Cultures; Ocean optics; Remote sensing

* Corresponding author. Mel Fisher Maritime Museum, 504 Bahama Street, Key West, FL 33040, USA. Tel.: +1-305-296-7657 or +1-207-633-2479; fax: +1-305-295-9536.
E-mail addresses: cyentsch@melfisher.org, cmyentsch@aol.com (C.M. Yentsch).

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1. Introduction

Even the casual observer notes the impressive effects of the Bahama Islands on the quantity and quality of upwelled-light. This is apparent from aircraft and in satellite imagery (Fig. 1). One concludes, and rightly so, that these islands by way of their optical

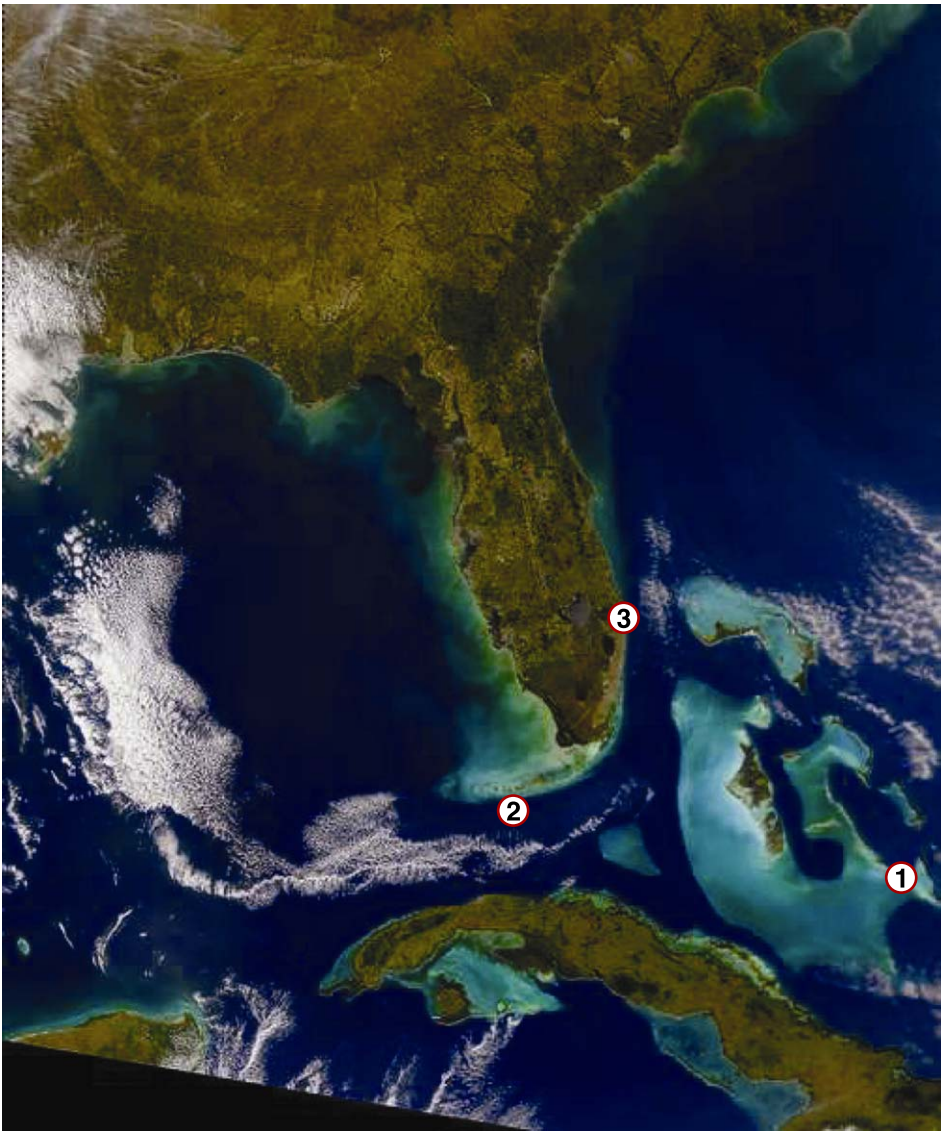

Fig. 1. Satellite image—Ocean Color image of South Florida, Cuba and the Bahamas on February 25, 1998 provided by the SeaWiFS Project, NASA/Goddard Space Flight Center, and ORBIMAGE, VE Record ID 5423. (1) Exuma Sound in the Bahamas off Lee Stocking Island, (2) the Florida Keys, Straits and, (3) coastal regions.

phenomena are one of the most important features of the southwestern Atlantic Ocean. The Bahamas are truly islands in the sea, surrounded by major ocean currents of the Atlantic drift. These waters, and those of the Florida Current, are classified as oligotrophic based on low concentrations of phytoplankton and nutrients. Hence, primary production and especially new production are low. Yet, the Bahamian and Florida platforms provide large areas of benthic autotrophic growth, which markedly attenuates sunlight, reduces the albedo, and changes the spectral signature of the upwelling light—all are characteristics of a rich productive ecosystem—how can this be?

Growth is not limited by light. Waters surrounding the Bahamian and Florida platforms, in the context of a terrestrial analogy, would be labeled a nutrient dessert. What are the nutrient sources for the biomass of this region? Where do the nutrients come from? How does this region fit into the paradigm of new production such as claimed for oceanic regions of the northwestern North Atlantic, i.e. the Gulf of Maine?

The present hypothesis of new production argues that in oligotrophic regions, it is the interaction between autotrophs and heterotrophs (grazing and decomposition), that regulates the cycling of the major nutrients such as ammonium nitrogen to the system. Production in this mode is recycled and thought of as ''in steady state''. Any new growth must come from elsewhere. New growth, therefore new production, would be by fixed nitrogen (NO_3-N) and nitrogen fixation (N_2). The sources for nitrogen in the subtropical and tropical waters are the large reservoirs in the deep oceans, rainfall, and the biological nitrogen fixation of atmospheric gas.

In 1963, Ryther introduced the term ''new production'' in Hill's treatise, THE SEA. The research gained recognition by studies on the uptake of nitrate and ammonium by Dugdale (1967) and Dugdale and Goering (1967). The earlier experiments at the Plymouth Laboratory summarized in Harvey (1955), and those of Harris, Riley and associates at the Bingham Laboratory extended the foundation of the oceanic mechanism of primary and new production. These addressed the important question of how primary production operates in the sea, first raised by Steeman Nielsen and Cushing (1958): Do low nutrient concentrations limit population size (i.e. nutrient limitation)? or is the efficiency of the physiological processes directly affected (i.e. nutrient deficiency)? In addition, the concept of new production was given further impetus by the introduction of the *f* ratio in McCarthy et al. (1975) and Eppley and Peterson (1979). This provided a useful dimensionless index by which areas of the oceans can be classified as to sources or sinks of carbon dioxide via either ammonium or nitrate uptake resulting in a first-order time and space estimate of oligotrophic and eutrophic regions of the oceans. The questions that emerge with the new production concept are: (1) the possibility that nutrients other than nitrogen (such as phosphate, iron and silicate) may limit growth, (2) the role of nitrogen fixation, (3) the recognition that a number of oceanic species (e.g. Prochlorophytes) cannot use nitrate and depend solely on ammonium (Andersen, personal communication).

Given these, we believe it is time to revisit the concept by a dialogue focussed on nutrient stress, following the research reviewed and synthesized by Parkhill et al. (2001). They focus on the validity of the measurement of variable fluorescence and its ecological value for the interpretation of nutrient stress. They have, knowingly or unknowingly, reawakened the debate surrounding the role of nutrient stress: is it limitation or deficiency?

Also at hand is a collegial debate on the old problem of: how far can one rely on culturing (batch vs. continuous) to interpret processes in nature?

We have some of the same goals as Parkhill et al. (2001) and have measured variable fluorescence on a variety of microalgae (cultures and natural populations) and collections of temperate and tropical macroalgae plus coral zooxanthellae. Our primary goals are ecological: (1) to determine the range of variable fluorescence for marine microalgae, macroalgae, and coral zooxanthellae, (2) to introduce some explanations for differences between Fv/Fm under batch culturing as opposed to continuous culturing conditions, (3) to offer our views on how the production of organic matter is regulated (limitation vs. deficiency) in marine photoautotrophs, and (4) to avoid getting caught up in the windy hypotheses of how photosystems work.

Why is an odyssey needed to do this? We believe that by visiting and comparing regions of the oceans where photoautotrophs thrive as opposed to regions where they do not can offer insights to the problems mentioned above. The backbone of the odyssey is a comparison of Fv/Fm in three geophysical realms. Within each realm, we use the trophic indicators: light transmission K (m^{-1}), surface chlorophyll and nitrate–nitrogen. For each realm, we present the major physical force for establishing nutrient/trophic conditions. We begin the odyssey by identifying the sites of the measurements, followed by the methods used and a discussion of the results from cultures and the field.

1.1. Scope of research program

Locations: Measurements of Fv/Fm were made on microalgae, macroalgae, and corals in the waters of Exuma Sound and shallow reefs around Lee Stocking Island, Bahamas (Lat. 23°50′ N; Long. 76°10′ W) during April and May 2001 and 2002. Measurements of Fv/Fm were measured in the Florida Straits off Key West (Lat. 24°30′ N; Long. 81°50′ W) and shoal reefs in October 2002–2003. Similar Florida coastal water measurements were made off Looe Key (Lat. 24°35′ N; Long. 81°25′ W) and off West Palm Beach (Lat. 26°40′ N; Long. 80°5′ W) in December 2001–October 2003. Fv/Fm was measured in the coastal waters off Boothbay Harbor, Maine (Lat. 44°0′ N; Long. 69°40′ W) in August and September 2002–2003. Fv/Fm was measured in axenic cultures from the CCMP at the Bigelow Laboratory in September 2003. Fv/Fm measured on coral planulae larvae was at Mote Marine Laboratory on Summerland Key in April 2002 and 2003.

1.2. Methodology of research

Variable fluorescence: The instrument we use for measuring Fv/Fm, the OSI-FL Modulated Chlorophyll Fluorometer, is made by Opti-Sciences. The fiber optic unit measures Fo (the minimal value when antennae are considered open and receptive of photons) and Fm (the maximum fluorescence emission after a pulse of light of saturating intensity that closes the antennae for light harvesting). A 35-W halogen lamp in the spectral range of 350–690 nm achieves saturation. The time of the saturating pulse is 0.8 s. The ratio of variable fluorescence (Fv) to the maximum fluorescence (Fm), therefore Fv/Fm=(Fm−Fo)/Fm, is calculated by the instrument internally, Fo, Fm and Fv/Fm are

presented on the monitor of the instrument as direct readings. A fiber optic cable carries both excitation and emission. The viewing end of the cable fits into a clip that holds the sample. The clip has a manually operated slide which when closed, darkens the specimen. Prior to measurement, samples were dark adapted for 5 min. The cable and clip are primarily designed to measure variable fluorescence from higher plant leaves in the field. It serves equally well for most macroalgae and microalgae retained on a membrane filter.

When concentrations of microalgae are low, the level of detection of the instrument can be met by concentrating the microalgae on a 2.5-cm GF/F glass fiber filter. For ocean observations, this amounts to filtration of 1–2 l of seawater. We feared that this might damage the cells and therefore affect the measurement. However, the comparison (Table 1) shows no obvious difference between the two methods of preparation/analysis. One benefit of the filter technique is that the problem of cells settling out in the cuvette is avoided, hence stirring is not necessary.

The dynamic range of Fv/Fm of our measurements appears identical to that obtained by the PAM fluorometer as reported by Parkhill et al. (2001). We have assigned the scale of 0.00–0.80 to correspond to 0–100%. In our opinion, fixing a range and scale is important for comparative purposes. The value of 0.80 is the highest that we have observed for marine photoautotrophs. It also approximates the theoretical value (Fo/Fm ~0.4–0.5) for isolated chloroplasts (Hock and Knox, 1968). Percentages of zero are measured (Fo=Fm) when specimens of microalgae, macroalgae, spinach, mangrove or banana leaves are placed in boiling water. Three readings are made on each sample and these values are averaged. If variability is high, additional measurements are made on the sample. The greatest variability was with low values of Fv/Fm. The estimation of the precision obtained is quite high (S.D.=0.05–0.10) for the entire data set used in this manuscript (n=>150).

Table 1
Fv/Fm measured on GF/F 2.5-cm filters and in suspension held in a glass cuvette, for three clones of microalgal cultures

Organism	Fv/Fm filter	Fv/Fm cuvette	Difference
Isochrysis sp.			
	0.648	0.581	0.067
	0.560	0.626	0.066
	0.557	0.602	0.045
Mean	0.588	0.603	0.059
Dunaliella tertiolecta			
	0.617	0.630	0.013
	0.618	0.591	0.027
	0.638	0.550	0.088
Mean	0.624	0.590	0.034
Skeletonema costatum			
	0.654	0.618	0.036
	0.605	0.518	0.087
	0.619	0.586	0.033
Mean	0.626	0.574	0.052

Comparison of Fv/Fm measured on microalgae using the filter method or directly in suspension.

To assess the effects of nutrient stress on cultures of microalgae, measurements of Fv/Fm were made on 13 clones of axenic microalgae held in culture at the Provasoli-Guillard National Center for the Culture of Marine Phytoplankton (CCMP) at Bigelow Laboratory for Ocean Sciences, courtesy of Dr. Robert Andersen. The cultures are routinely grown in F/2 medium in glass cotton-stoppered Erlenmeyer flasks at 22 °C under fluorescent irradiation (approximately 100 uEin/m^2) using a 12/12 photoperiod. To sustain the clonal cultures, they are routinely transferred to new F/2 media. Days or weeks may separate the transfers. For the measurements presented, the fiber probe was pressed against the side of the flask or test tube and the fluorescence measured following dark adaptation. In the event that the concentration of microalgae was too low to obtain a measurement, the algae were filtered onto a glass fiber filter and measured in that mode.

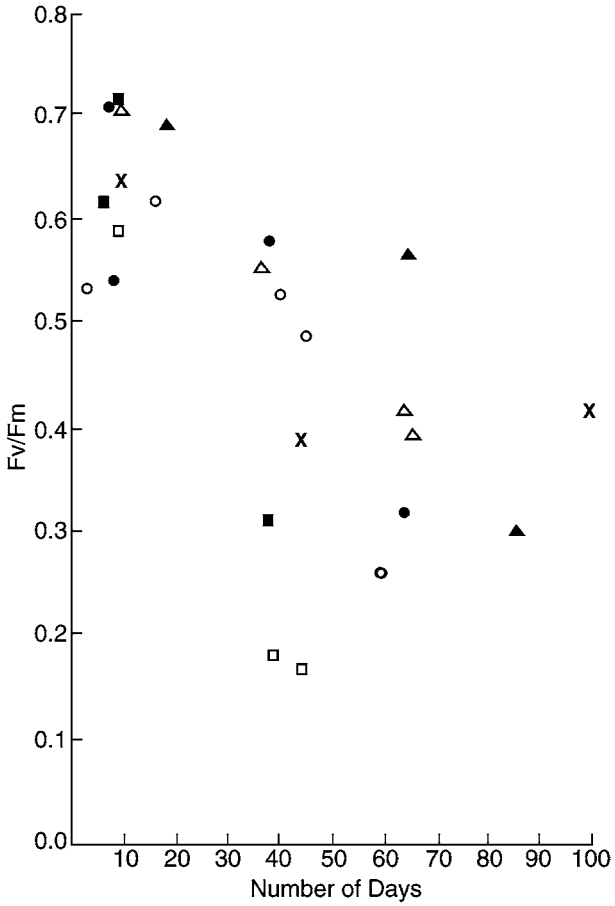

Fig. 2. Change of variable fluorescence (Fv/Fm) over time (days) for microalgal cultures from the CCMP. Samples were measured directly through the culture tube glass in a non-invasive manner. The various data points represent sequential transfers measured on the same date. Data for clones with three or greater data points have been used.

Collection of intertidal and subtidal macroalgae was made using a glass-bottom bucket or by SCUBA diving and snorkeling. Specimens were placed in plastic bags in a darkened bucket of seawater. Fluorescence measurements were made on site or in the laboratory in less than 1 h. All observations were made between 10 AM and 3 PM. Natural populations of microalgae were collected either by bucket surface sample or a Niskin water sampler. Samples were filtered and fluorescence measured. In some cases, water column and bio-optical measurements of down-welling light transmission using an International light IL1400 submersible photometer, peak wavelength 532 nm and extracted chlorophyll were measured along with salinity, temperature and depth of sampling.

Corals were collected under permit at Lee Stocking Island, and the Fv/Fm of zooxanthellae measurements were made directly on the intact coral community. Coral zooxanthellae within transparent planulae larvae were obtained courtesy of Dr. Jane Hawkridge at the Tropical Research Center of the Mote Marine Laboratory. The planulae were shed naturally from *Porites asteroides* and ranged in size from 50 to 600 um. The ones used for this study were all approximately 200 um. Planulae were individually isolated and several placed on a glass fiber filter and measured in that mode. Measurements were made April 20, 2002 and again in April and May of 2003.

2. Results

2.1. Microalgae cultures

Fv/Fm for 13 clones were measured. Disregarding the time of enrichment, the lowest Fv/Fm was observed to be 0.18 while the highest was 0.74. Both coastal and oceanic

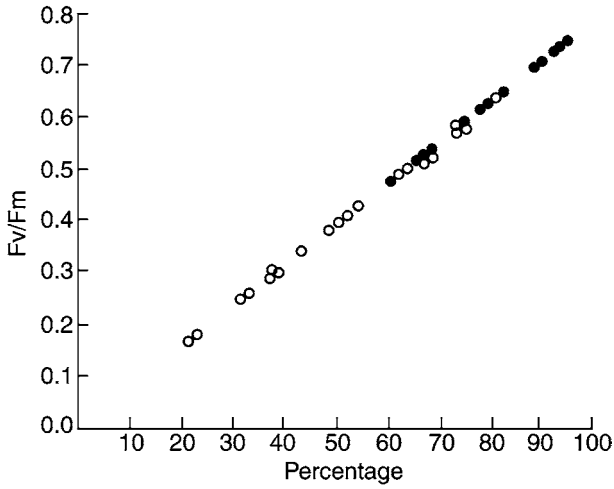

Fig. 3. Range of variable fluorescence (Fv/Fm) vs. percentage efficiency for microalgal cultures from the CCMP. Samples were measured directly through the culture tube glass in a non-invasive manner. Days indicate time since most recent transfer. The 2–20-day range (●) and the 30–100-day range (○).

clones were included. For some species, there were sufficient numbers of transfers to construct a crude time course (Fig. 2). For some, the Fv/Fm first increased approximately 10–20% after transfer. All were high (>60%) for 10–15 days after which the Fv/Fm declined for most of the clones after 30 days (Fig. 3). The time course data is too sparse, but the Fv/Fm for oceanic clones (*Prochlorococcus* sp.) appears to remain relatively higher than coastal clones over time. A significant point is that for many of the clones variable fluorescence remained high (0.40=50%) for more than 2 months. We measured variable fluorescence for the culture with the longest period without transfer. The record for the CCMP cultures measured goes to *Skeletonema tropicana* (50% after 100 days). In addition, among the large diatoms and dinoflagellates, *Coscinodiscus* sp. and *Alexandrium* sp. were recorded at 71 and 51 days, respectively. It has been noted that large non-axenic batch cultures of *Alexandrium tamarensis* have been kept "recycling" in the laboratory for years without nutrient enrichment (Yentsch, unpublished data).

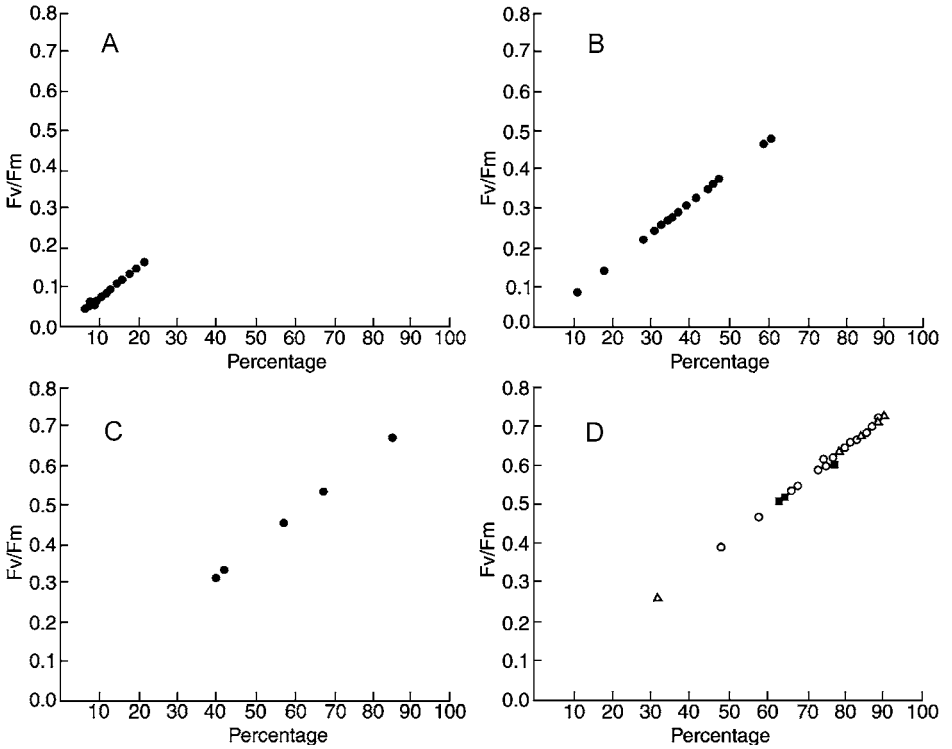

Fig. 4. Range of variable fluorescence (Fv/Fm) vs. percentage efficiency for natural populations of microalgae concentrated on GF/F filters for measurement and macroalgae. (A) Microalgae samples from Lee Stocking Island, Exuma, Bahamas. (B) Microalgae samples from the Gulf of Maine, Summer. (C) Microalgae samples from the Florida Straits and Florida Keys. (D) Macroalgae samples from Lee Stocking Island, Exuma, Bahamas and off West Palm Beach, FL. The open circle symbols represent green algae, triangles represent brown algae, and filled squares represent red algae.

2.2. Natural populations of microalgae

Variable fluorescence (Fv/Fm) for surface microalgae off Lee Stocking Island are very low (Fig. 4A). The values of 0.05–0.0.10 (10%) are the lowest we have measured. Fv/Fm at the base of the euphotic zone (120 m) was 10% higher than the surface (0.10–0.15, Yentsch and Phinney, unpublished data). For the microalgae in Florida surface waters, Fv/Fm ranges from 0.10 to 0.50 (10–60%) considerably higher than Bahamian populations. Values for the Straits of Florida off Key West centered around 0.24–0.32 (~40%) (Fig. 4B). Surface measurements near the North Wall of the Florida Current (0.26) were rich in *Oscillatoria* sp. *(Trichodesmium*) filaments (Yentsch, unpublished data). In shallow backcountry waters of patch reefs and mangroves, values were higher 0.30–0.50 (50–60%).

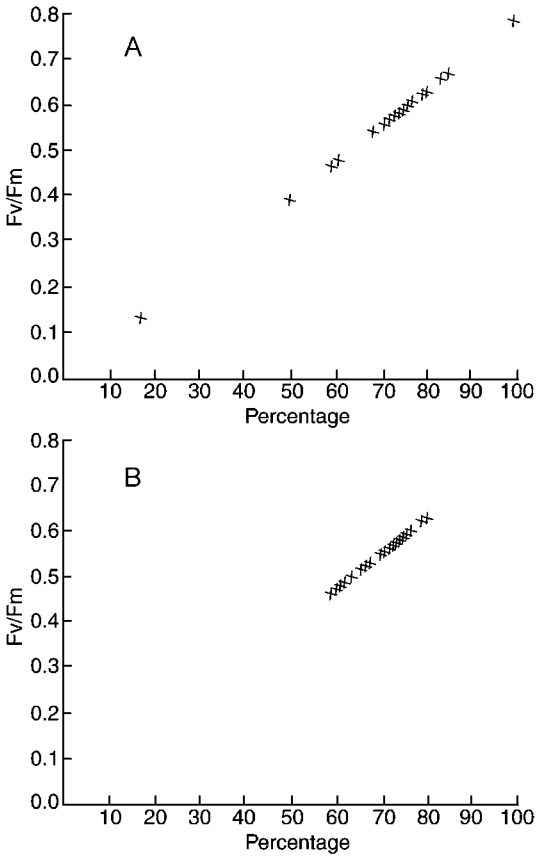

Fig. 5. Range of variable fluorescence (Fv/Fm) vs. percentage efficiency for natural populations of coral zooxanthellae (x). (A) Samples collected by permit from Lee Stocking Island. Measurements were made without manipulation on the mature polyp colonies containing the symbiotic zooxanthellae. (B) Data set of measurements from the coral zooxanthellae contained in planulae ciliated larvae (x). Planulae were released naturally and were handpicked and concentrated on a filter for Fv/Fm measurement.

In surface coastal waters off Boothbay Harbor, Maine, in August of 2003, the range observed was 0.30–0.70 (40–90%) (Fig. 4C). These values were measured in the region of a tidal front. The high values are on the shoreward side of a front and the low values are on the seaward side of the front.

2.3. Macroalgae, sea grasses and coral

With few exceptions, Fv/Fm for macroalgae and corals are considerably higher than those for natural populations of microalgae. Most of these species of macroalgae are intertidal algae, most were collected either in the Bahamas, Florida Keys or off West Palm Beach and Vero Beach, FL (Fig. 4D). In terms of the more northern temperate regions of Maine, we have measured Fv/Fm in *Laminaria* sp., *Ascophyllum* sp., *Ulva lactuca*, and *Monostroma* sp. These had Fv/Fm values around 0.70 (~80%). For the Bahamas, the range of Fv/Fm is 0.40–0.80 (50–100%) and the majority of the values occur between 0.65% and 100%. The high values of Fv/Fm (0.7–0.8) are largely dominated by Chlorophytes namely the genus *Caulerpa* sp., *Penicillus* sp., *Halimeda* sp., *Batophora* sp., and *Codium* sp. Measurements of floating *Sargassum* sp. are lower (0.30). However, most of the attached brown algae *Laminaria* sp. in the temperate waters and *Padina* sp. in the subtropical waters average ~0.60. Red algae averaged 0.50, and Fv/Fm measurements of the seagrass *Thallassia* sp. have a range of 0.40–0.70. Unfortunately, we have only limited measurements on these plants.

Zooxanthellae measured in healthy growing corals (Fig. 5A) and in coral planulae larvae concentrated on filters (Fig. 5B) were in the same range as the macroalgae (Fig. 5A,B). The majority of the measurements were between 0.50 and 0.80 (therefore, 60% to 100 %).

3. Discussion

The concept of new production has been fashioned by experimental biologists and supplied the basic knowledge of the relationship between nutrients and growth. We contend that the biology and physics cannot be uncoupled in the interpretation of physiology and ecology of photoautotrophs. There is great promise in the measurement of variable fluorescence for the modification of the new production paradigm.

The value of algal culturing for interpretation of nutrient stress: methods of culturing microalgae have been adopted that are believed to reproduce conditions in which photoautotrophs exist in the sea. Batch culturing is analogous to additions of nutrient by a vertical mixing event, i.e. a burst of nutrients in time. Steady state or continuous culturing is described as analogous to the nutrient recycling in the upper layers of a nutrient-impoverished ocean. Most believe both occur which is what was demonstrated by the ammonium enhancement of dark carbon fixation technique (Morris et al., 1971; Yentsch et al., 1977; Morris, 1980; Yentsch, 1977).

Understanding and predicting where and when both batch and continuous culture analogies are appropriate are major challenges to the value of the concept of new production and our ability to recognize nutrient stress. Parkhill et al. (2001) questions

the utility of the Fv/Fm method as a means for assessing nutrient stress which appears contrary to the opinions put forth by Gentry et al. (1989), Geider et al. (1993), Kolber and Falkowski (1993) and Cleveland and Perry (1987). Our experiments with CCMP algae agree with Parkhill et al., who have measured Fv/Fm in batch cultures. Our principal difference concerns the interpretation of Fv/Fm when a limiting nutrient is pulsed or provided in a steady state. This could be due to differences in species and/or perhaps methodology, other unknowns and/or various combinations of all of these.

The CCMP data dispels (for us) any measurable species-specific effect on Fv/Fm. However, the rate at which variable fluorescence in individual species declines to 50% differs markedly for these cultures. These were not controlled experiments and could reflect the differences in growth rate, cell quotient, maximum cell density and other unmeasured parameters. For the record, there is the suggestion from the data that the oceanic species may take a longer time getting to this point—this begs for further investigation. To us, what is amazing, is how long it takes for these organisms to go below 50%. This poses the question: when in time does a batch culture stop being a batch culture and revert to recycling? This point is important to the experimental differences of Parkhill et al. (2001) and Kolber and Falkowski (1993).

Might bacteria play a key role? Those maintaining axenic cultures do not vouch for bacterial-free status for long periods of time. Most of us, who have held cultures at some degree of prolonged senescence, experience bacterial and sometimes ciliate growth. This may be due to additions and removal of samples and the uncertainty of how well one separates bacteria from microalgae. After 30 to 50 days, one could conceive of the initial batch culture becoming a thriving ecosystem. Nutrient limitation vs. deficiency is fairly easy to demonstrate experimentally using cultures, but much more difficult in natural ecosystems.

From the ecological viewpoint, we question which is more significant, pulsed or continuous nutrient input? Considering the vast expanse of the oceans' area, continuous recycling might be considered the important process. However, with the advent of large data sets from satellite color imagery, especially SeaWiFs and MODIS, we believe that interpretation of the story may need changing. Even in the apparent solitude of the central gyres, there is a lot of pulsing going on. Observers at the open-ocean sites in the North Pacific (HOTS) and South Atlantic Gyres (BATS) are very aware of the coming and goings of eddies of all sizes (Lewis, 2002). This, coupled with the long-time period of survival under conditions of low nutrients provides new evidence for the frequency of pulsed events and their importance in primary production. Perhaps, pulsing has been underestimated.

We believe that the measurement of variable fluorescence is a powerful tool for the primary production pundits. We believe that it would be wrong to suppose that Fv/Fm alone could be a surrogate for the measurement of carbon fixation, but the evidence suggests it is can reflect nutrients and/or physiological status. Moreover, it must be stressed that the measurement is simple and rapid and requires no licensing and disposal of isotopes.

Consider this geophysical example: A trophic description based on the general geophysical signals indicates levels for eutrophic and oligotrophic conditions (Table

2). A three-dimensional block diagram of the region from Florida to seaward of the Bahamas (Fig. 2) implicates ocean current transport as a primary geophysical mechanism for regulating nutrient enrichment. The interpretation is that the low Fv/Fm values for the surface waters of Lee Stocking Island are due to the isolation of nutrient poor surface water from substantive nutrients in deeper waters. Why? This region is the stagnant part of the North Atlantic Gyre. The isopycnals are parallel to the isobars indicative of a slow barotrophic surface flow of the North Atlantic Drift (Leetmaa et al., 1977). The water masses have some of the highest surface temperatures and salinity, and the direction of prevailing winds is not favorable for upwelling. The nitrate/depth gradient has surface values of <0.10 to a depth 200 m which is approximately 100 m below the depth of the euphotic zone. Therefore, the trophic indicators for these oligotropic waters are high transparency (low K), and low surface chlorophyll and nitrate–nitrogen (Table 2).

The Lee Stocking Island zooxanthellae of corals are also microalgae. However, the symbiotic relationship with the coral polyp, or the property of being anchored, provides a unique nutrient environment that results in relatively high measurements of variable fluorescence, similar to the macroalgae. The high variable fluorescence for the free-swimming planulae larvae indicates that the photosystems of the dinoflagellates have the capacity for photosynthesis prior to settlement.

The values of Fv/Fm on the Florida side are two to three times higher than the values in Exuma Sound. Variable fluorescence of the microalgae from the surface water masses off the coast of Key West and mid-coast Florida populations have Fv/Fm of 0.20–0.40. The geophysical explanation offered is tied to the increased transport of the Florida Current through the Straits (Fig. 6). Reflecting this transport, the isopycnals slope upward to the left of the current direction thereby departing markedly from being parallel to the isobars.

Table 2
General trophic indices for areas where Fv/Fm measurements have been made

Location reference	Surface chlorophyll (μg/l)	Attenuation of downwelling light K (m^{-1})	Surface DIN (μmol/l)	Geophysical forces
(1) Exuma Sound Yentsch and Phinney, unpublished, off Lee Stocking Island	0.08–0.15	0.04–0.06	<0.1	Barotrophic=Baroclinic
(2) Florida Straits Yentsch et al., unpublished, off W. Palm Beach (Lapointe et al., in review)	0.05–1.0	0.07–0.08	<0.3	Baroclinic>Barotrophic
(3) Florida Keys, Yentsch et al., unpublished, off Key West (Lapointe et al., in review)	0.10–0.50	0.16–0.18	<0.50	Baroclinic>Barotrophic
(4) Gulf of Maine, Yentsch and Phinney, unpublished, off Boothbay Harbor	0.50–2.00	0.15–0.25	>1.0	Seasonal overturn, Tidal mixing

The trophic indicators for waters of Exuma Sound, Bahamas, Florida Keys, Straits and coast, and the Gulf of Maine off Boothbay Harbor.

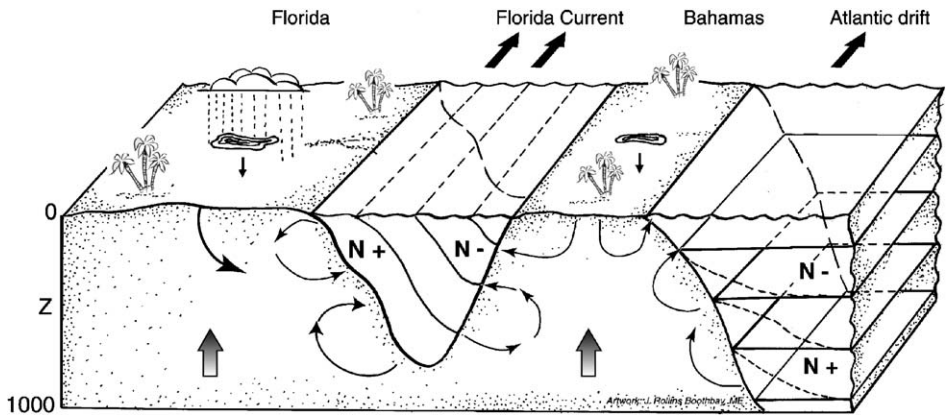

Fig. 6. The geophysical features in a three-dimensional cross-section from the State of Florida seaward to the Bahamas. This rendering depicts the major geophysical mechanisms for regulating nutrient enrichment which are isopycnal mixing and the suggestion of endothermic upwelling according to Rougerie and Wauthy (1993). The arrows on each platform represent earth heating.

In this case, the Florida coastal waters are potentially richer than those off the Bahamas. Their transparency is lower (high K), surface chlorophyll and nitrate higher (Table 2). The upward sloping isopycnals from deep water to euphotic depths provides nitrate values ~0.5 (μmol/L) in the surface waters 2.0 (μmol/L) at 100 m. All of our measurements of Fv/Fm>0.30 are in the shallow waters surrounding the Keys and Florida coastal regions.

As a point of eutrophic reference, the high Fv/Fm in Gulf of Maine waters reflects a higher level of nutrient input to microalgae (Table 2). Hence, there is lower transparency, high chlorophyll and surface nitrate. The forces here are seasonal overturn of water masses and by penetrative convection and tidal mixing. This combination allows for growth quiescence in the central gyres due to seasonal thermal stabilization and conditions of nutrient-replete conditions during seasonal turnover and in regions of tidal mixing.

There is no doubt in our minds with the data presented here that macroalgae and coral zooxanthellae are the most efficient in the capture and transfer of light energy. This undoubtedly accounts for their high rates of photosynthesis and growth. A frequency distribution histogram (using a bin size interval of Fv/Fm of 0.10) comparing all species measured from Lee Stocking Island is presented in Fig. 7. This clearly shows that the majority of Fv/Fm for macroalgae and corals overlap and are far greater than the microalgae. The former have 50–90% efficiency.

Many of the browns and some of the corals occupy the high end but it is the intertidal and subtidal green algae that are the highest. Of these, species of the genera *Caulpera* sp., *Entermorpha* sp., and *Codium* sp., stand out and are used as bioindicators of enrichment (Lapointe, 1997). The browns such as *Laminaria* sp. and *Ascophyllum* sp. run a close second. The reasons for these apparent high efficiencies are not clear. Since all spend most of their life history attached, the conventional concept of convective transport of nutrients seems appropriate. We have some data to support this: Fv/Fm on floating *Sargassum* sp., observed to be nutrient-starved (Lapointe, 1997). For floating fronds of *Thallassia* sp., Fv/

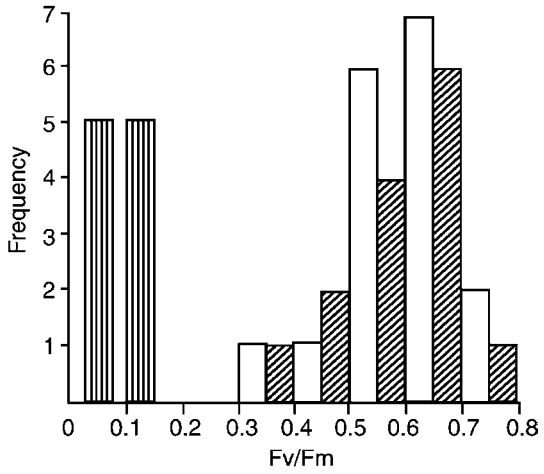

Fig. 7. Comparison of Fv/Fm for microalgae (vertical lines) and macroalgae (clear, no lines) and coral zooxanthellae (hatched lines), for samples from shallow waters off Lee Stocking Island.

Fm was less than 0.30 while attached algae was 0.60. Some species (e.g. *Caulpera* sp.) have root-like rhizomes that can absorb nutrients (Williams and Fisher, 1985). This provides an additional nutrient conduit through interstitial water in the sediments. In Fig. 6, we have sketched in the possible pathway termed endo-thermal upwelling. The interesting feature of this process is that this potential for nutrient transport utilizes the pool of nutrients in relatively rich, deep, ocean water. This seawater is forced upward, by the thermal heating from the interior of the platforms, and exits at more shallow depths. Which in theory could supply photoautotrophs at these depths. According to Tribble et al. (1994), this concept is insignificant for coral reefs. In the Bahamas, significant input of ground water when input at the surface, results in significant growth of macroalgae (Lapointe et al., in review).

Overall, the difference between floating in suspension and attached organisms may be the role played by diffusion to single cells in suspension. Regardless, a low Fv/Fm value we interpret to mean nutrient deficiency (a change in physiology) rather than nutrient limitation (a cap on cell growth or cell division). The beauty of the measurement of variable fluorescence is that it is independent of population size and perhaps, in the short term, the rate of growth. It would appear as a first-order inter-specific index.

The attempt to bring the macroalgae into the concept of new production in the oceanic sense is flawed in the subtidal zones where the distance of the light absorbing photosystem from the source of remineralization which regulates the new growth. The recognition of nutrient-deficiency as a physiological phenomenon means that the surface waters of the open ocean as compared to shallow coastal waters are not good for the photosynthetic processes because of nutrients and reduction of light by vertical mixing (Yentsch et al., 1977). If this were not so, there would be little or no need for continuing and advancing studies in new production and primary production.

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